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Post-weaning diet in archaeological human populations: a meta-analysis of carbon and nitrogen stable isotope ratios of child skeletons

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ABSTRACT

Objectives: Childhood is a unique stage in human life history, in which subadults have completed their weaning process but are still dependent on older individuals for survival. Although the importance of food provisioning during childhood has been intensively discussed, childhood diet in the past has rarely been studied in a systematic manner.

Methods: In this study, a meta-analysis of carbon and nitrogen stable isotope ratios of post-weaning children (PWC) in Holocene human populations around the world is presented. The isotope ratios of PWC were standardized with those of adult females and males in the same population, and they were analyzed in terms of the difference in subsistence.

Results: Results of this study indicate that diets of PWC and adults were generally similar (most differences were within the range of ±1‰), which is consistent with the universal feature of food provisioning to PWC in humans. In hunter–gatherer populations, there is no significant difference between PWC and adult isotope ratios. In non-hunter–gatherer populations, however, PWC probably consumed significantly larger proportions of foods from lower trophic levels than did the adults, and such foods would be terrestrial C_3 plants.

Conclusions: Potential factors relating to the dietary differences among PWC and adults are presented from a perspective of balance between food provisioning and self-acquisition by PWC. Significant isotopic differences between PWC and adults in non-hunter–gatherer populations revealed in this study have implications for declined health during the subsistence transition in Holocene, isotopic studies using human tooth enamel, and "$\delta^{15}N$ dip" of subadults after weaning.

Human childhood is a unique life history stage when compared to other non-human primates. First, human subadults demonstrate delayed maturity and take a longer time to acquire the physical and reproductive capacity of adults (Bogin and Smith, 1996; Bogin, 1997; Kaplan et al., 2000; Walker et al., 2006). The longer immature period in humans has been interpreted as a byproduct of a longer lifespan, required time for learning the complex skills of foraging, or a time to invest in the pooled energy budget (reviewed in Bliege Bird and Bird, 2002; Blurton Jones and Marlowe, 2002), although no single model completely explains the reason for the delayed maturity (Bird and Bliege Bird, 2000, 2002; Bliege Bird and Bird, 2002; Blurton Jones and Marlowe, 2002; Walker et al., 2002; Bock, 2005; Tucker and Young, 2013).

Theoretical frameworks for delayed maturity have been extensively evaluated in the fields of ethnology and evolutionary anthropology. Models explaining observed changes in behavioral characteristics with age in subadults, such as foraging skills, work effort, play, and balance between production and consumption, have been investigated (Bird and Bliege Bird, 2000, 2002; Bliege Bird and Bird, 2002; Blurton Jones and Marlowe, 2002; Kramer, 2002; Walker et al., 2002; Bock, 2005; Kramer and Greaves, 2011; Tucker and Young, 2013). These studies have demonstrated a great flexibility in behavioral ontogeny in the human immature period (Kramer, 2002; Kramer and Greaves, 2011).

The second point of uniqueness in human immature period, especially for younger childhood, is food provisioning from older individuals (Sellen, 2007). Routine food sharing is a universal feature of human populations (Jaeggi and van Schaik, 2011). While the cost of breastfeeding is covered mainly by mothers (but see Hewlett and Winn, 2014), food provisioning to post-weaning children can be done by others, which disperses the burden of childcare from mothers to other members of the population and the family. Although human children require food provisioning from adults, their relatively slower growth compared with infancy and adolescence (Bogin, 1997) makes the burden of food provisioning less severe (Gurven and Walker, 2006). Rather, children are immature in foraging skills, cognitive ability, and physical strength, and provisioned foods benefit the survival and health of children, especially if they are diseased or injured (Kaplan et al., 2000; Reiches et al., 2009; Kramer and Ellison, 2010). These characteristics of food provisioning during immature period enable a mother to invest more time and energy to future offspring and thus contribute to higher fertility rates without impairing the survival rates of offspring (Kramer, 2005, 2010; Gurven and Walker, 2006; Kramer and Ellison, 2010; Jones, 2011).

The importance of food provisioning to children in the evolution of human life history and behavioral ecology has been discussed in numerous studies (Bogin and Smith, 1996; Bogin, 1997; Kaplan et al., 2000; Kramer, 2005, 2010; Sellen, 2007; Reiches et al., 2009; Humphrey, 2010; Kramer and Ellison, 2010). Childhood diet is important for health and proper growth (Neumann et al., 2002), and some researchers hypothesized that children require carefully

selected and prepared nutrient-dense foods owing to their immature dentition and digestive systems (Bogin and Smith, 1996; Bogin, 1997; Humphrey, 2010; Bogin et al., 2016). However, actual diet in childhood has rarely been studied cross-culturally. This is because food acquisition is relatively easy to observe, yet food consumption is difficult because of sharing among family members and the disappearance after consumption (c.f., Haaga and Mason, 1987; Kramer and Greaves, 2011).

Childhood diet is formed by food provisioning and self-acquisition. The type and proportion of food sources included in the provisioning differs with culture and environment of the human populations. For example, adults who culturally value children may provide valuable foods, but harsh environments would not allow adults to collect a variety of foods in some cases. Children acquire foods by themselves in addition to provisioned foods (Konner, 2016). Because of their immature physical strength and skills, children usually adopt alternative foraging strategies and often obtain different food types than adults (Bird and Bliege Bird, 2000, 2002; Blurton Jones et al., 2002; Crittenden et al., 2013; Tucker and Young, 2013), as is the case with non-human primate juveniles (e.g., Pereira and Fairbanks, 2002; Nowell and Fletcher, 2007; Taniguchi, 2015; Mallott et al., 2017). Although acquired foods are typically shared in human societies, consumption before or without sharing is also observed (Blurton-Jones et al., 2002; Crittenden et al., 2013; Berbesque et al., 2016) and would lead to dietary differences between children and adults.

The subsistence transition from hunting and gathering to agriculture includes changes in staple foods, cultural traditions, demography, the behavioral environment (Weisdorf, 2005; Larsen, 2003, 2006; Bocquet-Appel, 2011), and also possibly childhood diet. Because childhood diets are related to several factors, cross-cultural meta-analysis is an efficient method of understanding the overview of the understudied childhood diet. However, the differences in childhood diets between those of hunter−gatherer (HG) and non-hunter−gatherer (NHG) archaeological human populations has never been studied systematically.

In this study, a systematic analysis of carbon and nitrogen stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$ values, respectively) of post-weaning children (PWC) in Holocene human skeletal samples around the world was presented to investigate whether there are dietary differences between children and adults. Although the isotope ratios of archaeological skeletons represent the diet of “non-survivors” (Wood et al., 1992), quantitative reconstruction of dietary proportions of actually consumed foods can be done by using the isotope analysis. The isotope ratios of PWC were standardized with those of adult females and males in the same sample, and they were analyzed in terms of the difference in subsistence, that is, HG and NHG.

Stable isotope analysis

Carbon and nitrogen stable isotope analyses have been used for dietary reconstruction in

archaeological human populations (Schoeninger and Moore, 1992; Katzenberg and Harrison, 1997; Lee-Thorp, 2008). The $\delta^{13}C$ values of plants vary depending on the type of photosynthesis; C_3 and C_4 plants indicate lower and higher $\delta^{13}C$ values, respectively (O'Leary, 1988), and this difference is incorporated into consumers higher in the ecosystem (Schoeninger and Moore, 1992; Katzenberg and Harrison, 1997; Lee-Thorp, 2008). The $\delta^{15}N$ values of an organism increase with the elevation of the trophic level, and some degree of increase in $\delta^{13}C$ values is also evident (Schoeninger and DeNiro, 1984). Organisms from a marine ecosystem usually manifest higher $\delta^{15}N$ values than those from a terrestrial ecosystem and higher $\delta^{13}C$ values than those from a C_3 ecosystem owing to the long food chains in marine environments (Schoeninger et al., 1983; Schoeninger and DeNiro,1984).

Nitrogen isotopes are also used to estimate weaning ages in past human populations (Humphrey, 2014; Tsutaya and Yoneda, 2015). Typically, the $\delta^{15}N$ values of subadult tissue increases 2‰−3‰, because breast milk is enriched in ^{15}N compared with the mother's diet, and decrease to adult values during and after the process of weaning (Fogel et al., 1989; Fuller et al., 2006). Weaning ages can be reconstructed by investigating the $\delta^{15}N$ change in subadult skeletons at different estimated ages (Tsutaya and Yoneda, 2015).

MATERIALS AND METHODS

Definitions

Referring to Bogin's works (Bogin and Smith, 1996; Bogin, 1997), age categories were defined as follows: infancy, the period when the mother provides all or some nourishment to offspring via breastfeeding (from birth to the end of weaning process); childhood, the period following the end of weaning, when the youngster still mostly depends on older people for feeding and protection (from the end of weaning process to 7 years); juvenile period, prepubertal period after the end of weaning (from the end of weaning to 10 years for girls and to 12 years for boys, including childhood). This classification is based on biological and not social definitions of age (Halcrow and Tayles, 2008; Sofaer, 2011).

Datasets

Original research articles of isotopic study on breastfeeding and weaning in archaeological human populations were searched with Google Scholar. Stable isotope ratios of subadults in archaeological human populations are usually reported systematically in research that targets reconstruction of breastfeeding and weaning practices. Keyword combinations for the Web searches comprised "breastfeeding," "weaning," "isotope," "infant," "child(ren)," and "subadult." Furthermore, the bibliographies in these articles were reviewed to obtain additional published articles. Articles that presented the numerical values for estimated age and bone collagen $\delta^{13}C$ and/or $\delta^{15}N$ values and included more than six subadult individuals were selected

for the analysis.

Isotopic data from 58 archaeological populations were obtained from a total of 55 publications (Table S1 and Figure S1). Information on the chronological period, location, and subsistence were obtained from the articles. Although the classification of subsistence is sometimes difficult to make unless existing dietary data are available and some samples indicate mixed-subsistence, the criteria used in this study is solely based on how they were defined by the original authors. The mean and standard deviation (SD) of adults were recalculated if their individual numerical values were reported; otherwise, the summarized values indicated in the articles were used. Populations with mean adult $\delta^{13}C$ values of < -13‰ and ≥ -13‰ were classified as populations subsisted mainly on C_3 and C_4 plants, respectively, for convenience. Five samples without a report on $\delta^{13}C$ values of adults (i.e., Aşıklı Höyük, Çayönü Tepesi, Josefov, Medici family, and Mikul˘cice: see Table S1) were classified as C_3 populations by considering their subadult $\delta^{13}C$ values, subsistence, chronological periods, culture, location, and/or ecosystem. A total of five C_4 samples were not used in this study because the widely variable $\delta^{13}C$ values of food sources, especially plants, in these samples would confuse the interpretation of the results. Although there were problems relating the non-independence of cultures, that is, Galton's problem (Mace and Pagel, 1994), the chronological period of the target samples spanned widely and the cultural continuity was difficult to assess. Therefore, all individual samples were treated as independent ones.

Before conducting the analyses, notable outlier individuals were excluded from the datasets by leave-one-out cross validation. Archaeological subadult skeletons sometimes indicate exceptional isotope ratios, possibly because of their early ages at the time of death, and such individuals should be omitted from the analysis. The 3SD ranges of isotope ratios were calculated after excluding one individual from each sample (leave-one-out validation), and if the individual was outside the 3SD ranges, this individual was marked as an outlier. This procedure of leave-one-out cross-validation and exclusion of outliers was performed independently for the $\delta^{13}C$ and $\delta^{15}N$ values in all samples. The number of samples with at least one outlier was 20 out of 46 (43.5%) and 12 out of 48 (25.0%) for $\delta^{13}C$ and $\delta^{15}N$ values, respectively. These denominators are the number of C_3 populations with reliable WARN calculations and a sufficient number of adult individuals (described below).

Isotope ratios of post-weaning children

The age when $\delta^{15}N$ signals of breast milk disappear from subadult bone collagen (t_2') was estimated for each sample by using the WARN package, version 1.1 (Tsutaya and Yoneda, 2013) in R software (R Core Team, 2015) to determine the onset of the post-weaning period (Figure 1). Because the turnover rate of bone collagen was comparatively slow, t_2' was later than the age at the end of weaning (Tsutaya and Yoneda, 2013). The WARN package calculated

the ages at the start and end of weaning by modeling the bone collagen turnover and $\delta^{15}N$ change in diet and subadult bone collagen (Tsutaya and Yoneda, 2013). The youngest age fulfilling the following condition was determined as t_2':

$$\delta^{15}N(t) \leq \delta^{15}N_{wnfood} + 0.1$$
$$(t = 0, 0.5, 1.0, 1.5, \ldots, 10.0),$$

where the modeled $\delta^{15}N$ values of bone collagen at a given age of *t* years were represented as $\delta^{15}N(t)$ (‰), and the $\delta^{15}N$ value for collagen synthesized from post-weaning foods is represented as $\delta^{15}N_{wnfood}$. 10,000 posterior parameter sets of weaning were computed by using the WARN package with default configurations (e.g., $t_1 \sim N(0.5, 3.0)$ and $t_2 \sim N(2.5, 3.0)$) for the prior distributions and 10,000 for the number of unit set of weaning parameters resampled (Tsutaya and Yoneda, 2013), which adopts approximate Bayesian computation; thus, 10,000 sets of t_2' ($t_2'^{(i)}$) were obtained for each sample. PWC were defined as individuals aged $t_2' \leq t \leq 8$ years old. Although the original definition of childhood by Bogin (Bogin and Smith, 1996; Bogin, 1997) contains subadults up to seven years old, the upper limit was set on eight years to increase the sample number, by considering the delay of bone collagen turnover. Human bone collagen at eight years old contains previous dietary signals, and bone from individuals between 7.0 to 8.0 years exhibit an approximately 1:1 ratio (Tsutaya and Yoneda, 2013). The mean and SD of t_2' of C_3 populations with reliable WARN calculations and sufficient number of adult and PWC individuals (described below) were 4.4 ± 1.5 years (n = 35) for $\delta^{13}C$ and 4.3 ± 1.5 years (n = 36) for $\delta^{15}N$ values.

Weighted average isotope ratios and the individual number of PWC were calculated by using 10,000 sets of t_2'. By averaging the isotope ratios and counting the individual number of PWC in every set of 10,000 t_2', 10,000 sets of mean carbon ($\delta^{13}C_C^{(i)}$) and nitrogen ($\delta^{15}N_C^{(i)}$) stable isotope ratios and number of PWC in $\delta^{13}C$ and $\delta^{15}N$ ($nC_C^{(i)}$ and $nN_C^{(i)}$) were obtained for each sample. The weighted means of $\delta_C^{(i)}$ by $n_C^{(i)}$ ($\delta^{13}C_C$ and $\delta^{15}N_C$) were used as representative values of the sample. To decrease the effect of the sometimes biased values of individual sets with few individual numbers of PWC, the weighted mean was used instead of the non-weighted mean. The average number of PWC individuals among the 10,000 sets for $\delta^{13}C$ and $\delta^{15}N$ (nC_C and nN_C) were also calculated and used for quality control (described below).

The weighted mean isotope ratios of PWC were standardized with the adult values to enable inter-sample comparison. The mean isotope ratios of adults were obtained from both females ($\delta^{13}C_F$ and $\delta^{15}N_F$) and males ($\delta^{13}C_M$ and $\delta^{15}N_M$). The differences in isotope ratios (Δ values) between PWC and adult females/males were calculated as follows, respectively:

$$\Delta_{C\text{-}F} = \delta_C - \delta_F, \text{ and}$$
$$\Delta_{C\text{-}M} = \delta_C - \delta_M.$$

Quality controls and exception handling

Three types of quality controls were applied to the dataset to exclude unreliable data. First, four samples with obviously unreliable results from the WARN calculation were excluded from the dataset (Table S2). Second, the mean values of adult females or males calculated from less than three individuals were coded as "Not Available" because such a mean could be biased from individuals exhibiting exceptional isotope ratios. The mean isotope ratios of adult females (n = 2) and males (n = 1) from one sample (Triberga: see Table S1) were coded as "Not Available." Finally, δ_C calculated with less than two PWC individuals on an average (i.e., nC < 2) were excluded because the $\delta^{13}C_C$ and $\delta^{15}N_C$ values calculated from a few individuals could bias the results.

Several types of quality controls for the dataset described above are summarized here. First, five C_4 populations out of 58 with over -13‰ of adult $\delta^{13}C$ values were not used in this study. Second, one sample with less than three adult individuals was excluded from the remaining 53 samples. Third, four samples out of 52 with obviously unreliable results from WARN calculations were excluded (Table S2). Among these 48 samples, $\delta^{13}C$ values of subadults were not reported in two of the samples. Finally, δ_C calculated with less than two PWC on an average were excluded: 11 samples out of 46 for $\delta^{13}C$ and 12 samples out of 48 for $\delta^{15}N$ values. Therefore, the actual dataset consisted of 35 and 36 samples for $\delta^{13}C$ and $\delta^{15}N$ values, respectively. However, the sample size varied further by the type of analyses because some samples lacked isotope ratios of adult males or both adult females and males (See Table S3).

Exceptional cases of data handling for two samples is described here. First, to conduct WARN calculations for the Isola Sacra (see Table S1), the prior distributions were set to $t_1 \sim N(0.0, 1.0)$ and $t_2 \sim N(1.0, 1.0)$ because this sample had the unique features of younger weaning ages and higher E values, which complicated the parameter optimization (see Tsutaya and Yoneda, 2013). Next, for the Meuse (see Table S1) with individuals from different three periods (from Mesolithic to Neolithic), the WARN program was applied to subadults from all three periods, but subsequent analyses were performed only on subadult and adult individuals from the Ancient Mesolithic period, wherein a sufficient number of child and adult female individuals existed (but not enough for a WARN calculation).

Statistics

The following three topics were analyzed in the dataset:

1. the systematic difference between adult females and males ($\Delta_{M\text{-}F}$)
2. the systematic difference between PWC and adult females or males ($\Delta_{C\text{-}F}$ and $\Delta_{C\text{-}M}$, respectively)
3. the relationship between the PWC−adult difference ($\Delta_{C\text{-}F}$ and $\Delta_{C\text{-}M}$) and other variables, such as the adult isotope ratios ($\delta_{F/M}$).

Mann−Whiteney U tests were applied to topics 1 and 2 because the data do not follow a normal

distribution. Linear modelings (LMs) and Spearman's rank correlation tests were applied to topic 3. The explanatory variables of LM were adult female/male isotope ratios ($\delta^{13}C_{F/M}$ and $\delta^{15}N_{F/M}$), PWC−adult female/male differences in different isotopes (e.g., $\Delta^{15}N_{C\text{-}F/M}$ for $\Delta^{13}C_{C\text{-}F/M}$), and the age when the $\delta^{15}N$ signals of breastmilk disappeared from subadult bone collagen (t_2'). Models were constructed independently for HG and NHG populations. Best-fit models were selected based on the Akaike's information criterion (Akaike, 1973). All analyses were performed by using R software, version 3.2.3 (R Core Team, 2015). The significance level was set as $\alpha = 0.05$.

RESULTS

Sex differences in adults

Mean isotope ratios of adult males tended to be higher than those of adult females especially in the NHG populations (Figure 2 and Table 1, see Table S3 for raw data), although the male−female differences ($\Delta^{13}C_{M\text{-}F}$ and $\Delta^{15}N_{M\text{-}F}$) are relatively small (mostly within ±1‰) in terms of trophic level effect. Paired Mann−Whitney U tests indicated significantly higher $\delta^{13}C$ and $\delta^{15}N$ values of the males in the NHG populations (Table 3). Yet, the paired Mann−Whitney U tests indicated no significant sex difference in $\delta^{13}C$ and $\delta^{15}N$ values in HG populations (Table 1).

Differences between PWC and adults

The weighted mean isotope ratios of PWC tended to be lower than the mean isotope ratios of adults (Figure 3 and 4 and Table 2, see Table S3 for raw data), although the difference in the isotope ratios between PWC and adult females ($\Delta_{C\text{-}F}$) and between PWC and adult males ($\Delta_{C\text{-}M}$) were relatively small (mostly within ±1‰) in terms of trophic level effect. The carbon and nitrogen isotope ratios of the PWC in the HG population were lower than those of the adult females and males on an average (see Figure 4), but the differences were not significant (paired Mann−Whitney U tests: Table 2). The stable isotope ratios of PWC in the NHG populations were lower than those of the adults on an average (Figure 4), and the paired Mann−Whitney U tests indicated a significant difference for carbon and nitrogen isotopes when compared with males and a significant difference for carbon isotope when compared with females (Table 2).

As expected from the differences between adult females and males, mean isotopic differences between PWC and adult males are larger than those between PWC and adult females for both HG and NHG populations (Table 3). Paired Mann−Whitney U tests indicated a significant difference for $\delta^{13}C$ and $\delta^{15}N$ differences in NHG populations, but not in the HG populations (Table 3).

Relationships among variables

The best-fit linear models indicated a negative explanatory power of adult $\delta^{13}C$ values for the variation in the PWC−adult $\delta^{13}C$ differences in the NHG populations (Table 4). The models also indicated positive relationships between the PWC−adult differences of carbon and nitrogen in the HG females and NHG males (Table 4). The $\Delta^{15}N_{C\text{-}F}$ values of NHG females are not explained by other variables. The LM could not be applied to the $\Delta_{C\text{-}M}$ values of the HG males owing to its smaller sample size (n = 3).

Correlation tests provided further support for the systematic variation between $\Delta^{13}C_{C\text{-}F/M}$ and $\delta^{13}C_{F/M}$ values in the NHG populations: lower $\Delta^{13}C_{C\text{-}F/M}$ for higher $\delta^{13}C_{F/M}$ (Figure 5). Spearman's rank correlation tests indicated a significant negative correlation between $\Delta^{13}C_{C\text{-}F/M}$ and $\delta^{13}C_{F/M}$ in NHG populations ($\Delta^{13}C_{C\text{-}F}$ and $\delta^{13}C_F$: R = -0.474, P = 0.017, n = 25; $\Delta^{13}C_{C\text{-}M}$ and $\delta^{13}C_M$: R = -0.731, P < 0.001, n = 21). In contrast, there is no significant correlation in the HG populations (Spearman's rank correlation test: $\Delta^{13}C_{C\text{-}F}$ and $\delta^{13}C_F$: R = -0.071, P = 0.906, n = 7; $\Delta^{13}C_{C\text{-}M}$ and $\delta^{13}C_M$: R = -1.000, P = 0.333, n = 3): relatively constant $\Delta^{13}C_{C\text{-}F/M}$ for varying $\delta^{13}C_{F/M}$ (Figure 5). There was no systematic variation between the $\Delta^{15}N_{C\text{-}F/M}$ and $\delta^{15}N_{F/M}$ values for both the HG and NHG populations (Figure S2).

Spearman's rank correlation tests did not indicate significant correlation between the maximum density estimator for the age at the end of weaning calculated by the WARN program and $\Delta^{13}C_{C\text{-}F/M}$ or $\Delta^{15}N_{C\text{-}F/M}$ values for both HG and NHG populations (Figure S3).

DISCUSSION

Interpretation of the results

Although $\delta^{15}N$ values of organisms vary owing to physiological reasons, the concurrent change in the $\delta^{13}C$ and $\delta^{15}N$ values in the same direction can generally be regarded as a result of diet, more specifically, different proportions of food consumption between lower and higher trophic levels. The $\delta^{15}N$ values of an organism decrease because of pregnancy (Fuller et al., 2004; Nitsch et al., 2010) and growth (Waters-Rist and Katzenberg, 2010; Reitsema and Miur, 2015), increase because of nutritional stress (Fuller et al., 2005; Mekota et al., 2006), and vary because of skeletal indicators of stress and disease and related bone remodeling (Katzenberg and Lovell, 1999; Olsen et al., 2014). However, the $\delta^{13}C$ values indicate no systematic change due to these factors (Reitsema, 2013). In contrast, different proportions of food consumption between lower and higher trophic levels would result in a concurrent change in the $\delta^{13}C$ and $\delta^{15}N$ values in the same direction because these foods usually differ both in $\delta^{13}C$ and $\delta^{15}N$ in the same direction (e.g., C_3 plants vs. terrestrial animals and C_3 terrestrial foods vs. marine foods) (Schoeninger et al., 1983; Schoeninger and DeNiro, 1984; Schoeninger and Moore, 1992; Katzenberg and Harrison, 1997; Lee-Thorp, 2008).

In this regard, systematic dietary differences within a population were more evident in the NHG populations than in the HG populations from the results of this study. There was no

systematic isotopic difference between adult females and males in the HG populations, but the former showed significantly lower $\delta^{13}C$ and $\delta^{15}N$ values than the latter in the NHG populations (Table 1 and Figure 2). In both populations, the isotope ratios of PWC were lower than those of adult females and males, and the difference was larger when compared with males, although these differences were not significant in the HG populations (Table 2 and 3, and Figure 4). These differences suggest that the dietary proportions of foods from higher trophic levels tended to be significantly smaller in PWC, adult females, and adult males in sequence in the NHG populations, but this is not the case in the HG populations. However, note that these differences were relatively small in terms of trophic level effect, and the diet of PWC, adult females, and adult males were generally similar, even in the NHG populations.

Significant negative correlations in $\Delta^{13}C_{C\text{-}F}-\delta^{13}C_F$ and $\Delta^{13}C_{C\text{-}M}-\delta^{13}C_M$ were evident in the NHG populations (Figure 5). Provided that the repertoire of dietary items was the same between PWC and adults, these negative correlations indicated that the higher the $\delta^{13}C$ values of diet appeared in NHG populations, the larger the proportion of foods with relatively low $\delta^{13}C$ value were consumed by PWC. This relationship was absent in the HG populations, and the proportion of consumed food with relatively low $\delta^{13}C$ value did not systematically vary by the $\delta^{13}C$ value of the adults in the HG populations (Figure 5).

These negative correlations suggest that the proportions of terrestrial plant foods in a PWC diet were larger than those in the adults' diet in the NHG populations but not in the diets of the HG populations. Relative $\delta^{13}C$-differences of terrestrial C_3 plants were typically larger when compared with foods from higher trophic levels (e.g., marine, freshwater, and terrestrial animal foods) (Schoeninger et al., 1983; Schoeninger and DeNiro, 1984; Schoeninger and Moore, 1992; Katzenberg and Harrison, 1997; Lee-Thorp, 2008), and the decrease in PWC $\delta^{13}C$ values owing to the consumption of terrestrial C_3 plants would be more pronounced in populations that subsisted with foods from higher trophic levels, even if the increased proportion of terrestrial plants in the PWC diet was the same among populations. The availability of terrestrial crops such as cereals and vegetables would be high in NHG populations (Larsen, 2003). Although terrestrial plant foods usually show lower $\delta^{15}N$ values than foods from higher trophic levels, $\delta^{15}N$ values of consumer tissues are not affected much owing to the low concentration of nitrogen atoms in these foods (Phillips and Koch, 2002). This would be the reason why the negative correlations were observed only in the $\delta^{13}C$ values but not in the $\delta^{15}N$ values. Alternatively, it is possible that the $\delta^{15}N$ values were also affected by the physiological conditions of the individuals, such as nutritional status (Fuller et al., 2005; Mekota et al., 2006), stress and disease (Katzenberg and Lovell, 1999; Olsen et al., 2014), or pregnancy (Fuller et al., 2004; Nitsch et al., 2010), and do not reflect pure dietary signals.

In summary, the results of this study indicate that diets of PWC and adults were generally similar, which is consistent with the universal feature of food provisioning to PWC in humans

(Kaplan et al., 2000; Reiches et al., 2009; Kramer and Ellison, 2010). In the HG populations, there is no significant difference in trophic levels between PWC and adults' diet (Table 2 and Figure 4). However, in the NHG populations, PWC consumed a significantly larger proportion of food from lower trophic levels than the adults, and such foods would be terrestrial C_3 plants (Table 2 and Figure 4 and 5).

Sex difference in adults

Although a detailed discussion of the observed isotopic differences between female and male adults is beyond of the scope of this study, possible reasons for this difference are presented below. First, it is possible that it is easier for males than for females in NHG populations to access foods from higher trophic levels through cultural norms, such as ritual proscriptions, sexual division of labor (Murdock and Provost, 1973; Berbesque et al., 2011, 2016), and culturally ascribed male dominance (Quinn, 1977; Mukhopadhyay and Higgins, 1988; Umezaki et al., 2016). Second, sex differences in food preference (Berbesque and Marlowe, 2009) and changes in food preference and consumption during pregnancy (Faas et al., 2010) would result in sexual differences in dietary consumption. Although we should consider the complex spectrum of human gender and sex and be careful not to simply adopt biological determinism (Mukhopadhyay and Higgins, 1988; Sofaer, 2006; Hollimon, 2011), the isotopic difference between sexes is less well-studied cross-culturally and is an important future topic.

Probable causes of the difference between PWC and adults

Further investigation of the causes and consequences of dietary differences were difficult owing to the limited sample size and information in the archaeological dataset. However, the potential factors that related the dietary differences between PWC and adults were inferred. The diet of PWC is formed by food provisioning and self-acquisition. The former would be affected by gender asymmetry and cultural beliefs, and the latter would be affected by behavioral and physiological characteristics of PWC.

Gender asymmetry is one of the probable causes of the dietary difference between PWC and adults in the NHG populations. Most of the childcare responsibility is covered by females in most human population around the world (Brown, 1970; Murdock and Provost, 1973; Quinn, 1977; Mukhopadhyay and Higgins, 1988). Because food provisioning is a part of childcare, it is reasonable that the diet of PWC is more similar to that of adult females than that of adult males in both the HG and NHG populations (Table 3). In addition, father−child proximity is generally higher in HG populations than in NHG populations (Marlowe, 2000). If we assume that the proximity represents the degree of childcare efforts, the higher proximity in HG populations is consistent with the results showing that there is no significant difference between PWC and adult males in the HG populations but showing there is a difference in the NHG

populations (Table 3).

Cultural beliefs about what foods should be provided to subadults affect the diet of PWC. Although there has been no systematic analysis about the diet of PWC, several ethnographic and isotopic studies indicated that provisioned foods during the weaning process mostly consisted of foods from relatively lower trophic levels, such as plants. A meta-analysis of ethnographic studies indicates that subadults in the NHG populations were significantly more likely to be fed by milk and crop-derived foods rich in carbohydrates and were significantly less likely to be fed meat, fish, and fruits than subadults in HG populations during the weaning process (Sellen and Smay, 2001). This trend of crop preferences as weaning foods in NHG rather than in HG populations also appears in the isotopic case studies of archaeological human populations. For example, it was estimated that rice gruel was mainly used as weaning food in NHG populations in Hitotsubashi (1657−1683 AD, Japan: Tsutaya et al., 2014) and cereals were used as weaning food in Isola Sacra (1−3 centuries AD, Italy: Prowse et al., 2008), respectively, but marine animal products and terrestrial C_3 plants were used as weaning food in HG populations in Moyoro (5−13 centuries AD, Japan: Tsutaya et al., 2015b) and terrestrial animal products and terrestrial C_3 plants were used in HG populations in Lake Salitroso (800−300 BP, Argentina: Tessone et al., 2015). In general, C_3 terrestrial plants such as most crops and cereals have lower $\delta^{13}C$ and $\delta^{15}N$ values than marine and terrestrial animal products (Schoeninger et al., 1983; Schoeninger and DeNiro, 1984; Schoeninger and Moore, 1992; Katzenberg and Harrison, 1997; Lee-Thorp, 2008). It would be reasonable to assume that PWC are along the dietary or cultural continuum of weanlings and provisioned by similar diets. Results of this study are consistent with the evidence (see Table 2, Figure 4 and 5). Some ethnographic studies have demonstrated uneven food distribution among family members, where subadults tend to receive relatively lower energy or protein than adults (reviewed in Haaga and Mason, 1987).

The self-acquisition of specific foods by children also affects the isotopic difference between PWC and adults. Human children are not passive agents but are actively involved in food production and acquisition usually from an early age (Rogoff et al., 1975; Kramer, 2005, 2010). For example, the Hadza children and juveniles in an HG population in a savanna−woodland habitat in Northern Tanzania were able to obtain 25%−100% of their daily caloric needs (Crittenden et al., 2013; Crittenden, 2016). However, because of their immature physical strength and skills, subadults tend to adopt different foraging strategies or engage in different food production activities than adults, resulting in the acquisition of consistently different foods by PWC compared with adults (Bird and Bliege Bird, 2000, 2002; Blurton Jones et al., 2002; Crittenden et al., 2013; Tucker and Young, 2013). If the acquired foods were consumed before or without sharing, the self-acquisition of specific foods possibly may result in isotopic difference between PWC and adults. Although there are not many ethnographic studies of food

consumption before sharing, consumption of self-acquired foods or snacks before/without sharing is evident in some human populations (Blurton-Jones et al., 2002; Crittenden et al., 2013; Berbesque et al., 2016).

Physiological food preferences in subadults differ from those of adults, which would affect food consumptions in PWC, as well as their immature dentition and digestive systems (Bogin and Smith, 1996; Bogin, 1997). Human subadults typically prefer sweet and fatty foods and dislike bitter ones, and their taste preferences are directly connected with food consumption; however, this is not the case with adults (Birch, 1992; Drewnowski, 1997). These tendencies were learned and developed during ontogeny and come to less prominence when the individuals have grown (Drewnowski, 1997; Birch and Doub, 2014).

Implications of this study

The results of isotopic differences between PWC and adults in this study have implications for subsistence transition during Holocene, isotopic studies using human tooth enamel, and "δ^{15}N dip" of subadults after weaning. First, the consumption of relatively larger proportions of food from lower trophic levels in PWC of NHG populations was possibly related to decline in skeletal health after the onset of agriculture. During the Holocene, the subsistence transition from hunting and gathering to agriculture occurred throughout the world and usually corresponded with increased nutritional stresses and diseases on human skeletons (Larsen, 2003, 2006). Animal source foods are important for health and proper growth of subadults (Neumann et al., 2002), and the results of this study suggest that the relative proportion of animal foods compared with adults in the same population is smaller in PWC in NHG populations. Although the isotope ratios are indicators of relative, not absolute, proportions of consumed food sources, it is possible that the reduced health of agricultural populations in early stages stems from a subadulthood diet with further fewer amount of animal foods (c.f., Larsen, 2003).

Second, although δ^{13}C values of human tooth enamel have been measured to reconstruct past diets (Lee-Thorp, 2008; Schoeninger, 2014), the results of this study suggest that reconstruction of an adult diet using tooth enamel can be biased when using a specific type of teeth. Some parts of the enamel in some types of teeth (e.g., permanent second molars) are formed during the PWC period (Hillson, 1996), and dietary differences between children and adults would sometimes appear in this period, especially in NHG human populations. When discussing adult diet with isotope ratios of these enamels, the possibility of deducing a slightly different diet during PWC periods should be considered.

Third, the results of this study suggest that diet, not positive nitrogen balance during growth, was the principal cause of "δ^{15}N dip" in subadults. A decrease in δ^{15}N values of subadults just after the end of weaning period ("δ^{15}N dip") has been observed in isotopic results obtained from both living and skeletal materials. This was interpreted as a result of positive nitrogen balance

during the subadult growth or consumption of foods from lower trophic levels, different than that of adults, but the reported evidence has been controversial (Waters-Rist and Katzenberg, 2010; Reitsema and Muir, 2015). The results of this study support the hypothesis that there was a dietary difference between PWC and adults because the concurrent decrease in $\delta^{13}C$ and $\delta^{15}N$ values in PWC compared with adults (Figure 3) suggests a change in the dietary proportion of foods from different trophic levels. If the hypothesis of positive nitrogen balance were correct, only $\delta^{15}N$ values would differ.

Limitations of this study

There are several limitations in this study. First, the isotope ratios of subadult bone collagen represent the diet of individuals who died at a subadult age. If diets differ between individuals who have died and those who survived, the results obtained from dietary reconstruction using subadult skeletons would be biased (Beaumont et al., 2015). It is possible that the cause of the death is dietary, and survived individuals in the NHG populations actually consumed adequate proportion of foods from higher trophic levels (c.f., Sandberg et al., 2014; Reitsema et al., 2016). Comparison with results from meta-analysis of the isotope ratios of teeth, which record childhood diet of survivors, is the interesting future topic.

Second, the skeletal remains of adult females, adult males, and children are not necessarily mothers, fathers, and offspring, respectively. Isotopic comparison among actual family members are needed, but fairly difficult for archaeological materials, for more rigorous investigations on the cultural and behavioral factors behind isotope ratios.

Third, the results presented in this study are only applicable for inter-population comparisons; they are not applicable for comparing individuals within one population (Pollet et al., 2015). For example, the distribution of isotope ratios among individuals in a population was not considered and isotopic correlations observed among populations cannot necessarily be observed among individuals in one population.

Fourth, using a small sample size of HG populations is problematic. It is possible that a true difference was not detected because a small statistical power might have resulted from using a small sample size of HG populations. However, a sufficient number of subadult skeletons are rarely found at archaeological sites of HG populations because their members usually lived in lower population densities than NHG populations.

Finally, discussing nutritional status from the results of this study is difficult because the isotope ratios only reflect a proportion of dietary items but not quantities. Furthermore, the $\Delta_{C\text{-}F/M}$ values only represent a relative difference of PWC diet compared with adult diet in the same population and are not the indicator of inter-population differences of nutritional status during childhood. The relationships between nutritional status and demographic profiles (i.e., fertility inferred from the age at the end of weaning) in skeletal populations are of interest regarding the

subsistence transition during the Holocene (Buikstra et al., 1986; Lee et al., 1991; Lambert, 2009). However, nutritional status during childhood should be evaluated from other measure than the $\Delta_{C\text{-}F/M}$ values, such as skeletal indicators of stress and disease. Nonetheless, this study indicates that there was no significant relationship between the age at the end of weaning and $\Delta_{C\text{-}F/M}$ values for both HG and NHG populations (Figure S3).

CONCLUSIONS

This is the first study to systematically analyze the diet of archaeological post-weaning children which has an important role in the evolution of human life history. Results of this study indicated that diets of PWC and adults were generally similar (most differences were within the range of ±1‰). However, in NHG populations, PWC probably consumed significantly larger proportions of foods from lower trophic levels than did the adults, and such foods would be terrestrial C_3 plants. Detailed ethnographic and bioarchaeological studies concerning childhood diet are important to investigate the causes and consequences of slightly different diets of PWC in the context of the evolution of human behavioral ecology and demographic changes around subsistence transition in Holocene, respectively.

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FIGURES

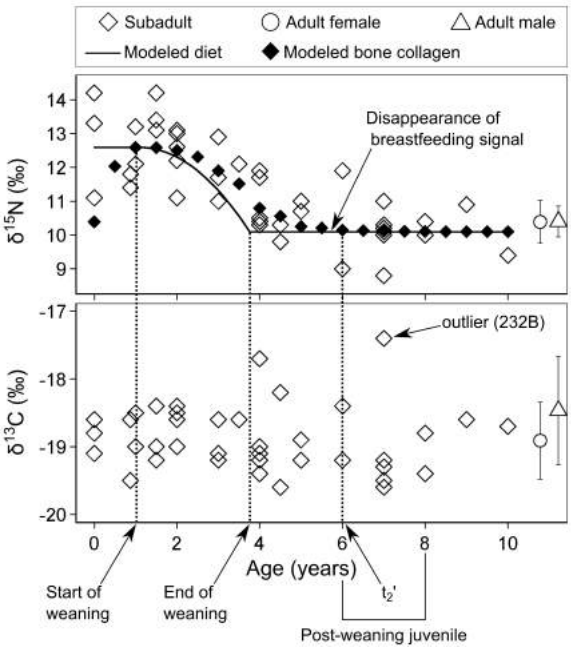

Figure 1. Schematic illustration for the determination of PWC. Subadult ages and bone collagen isotope ratios were obtained from Yuigahama-minami population (12−14 centuries AD, Japan: Tsutaya et al., 2015a).

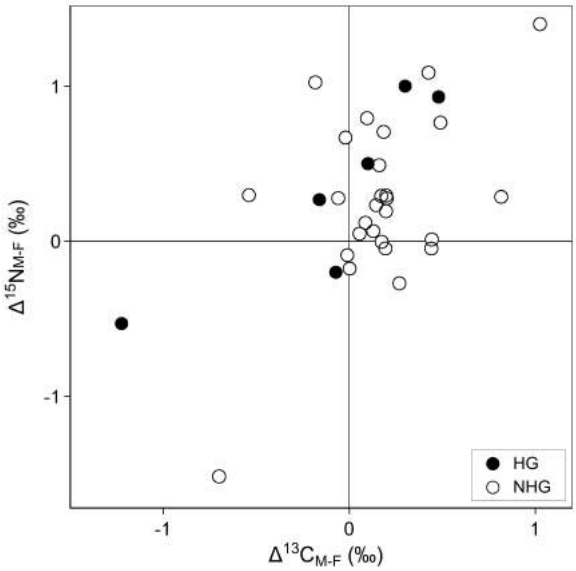

Figure 2. Scatterplot of $\delta^{13}C$ and $\delta^{15}N$ differences between adult females and males for the archaeological populations.

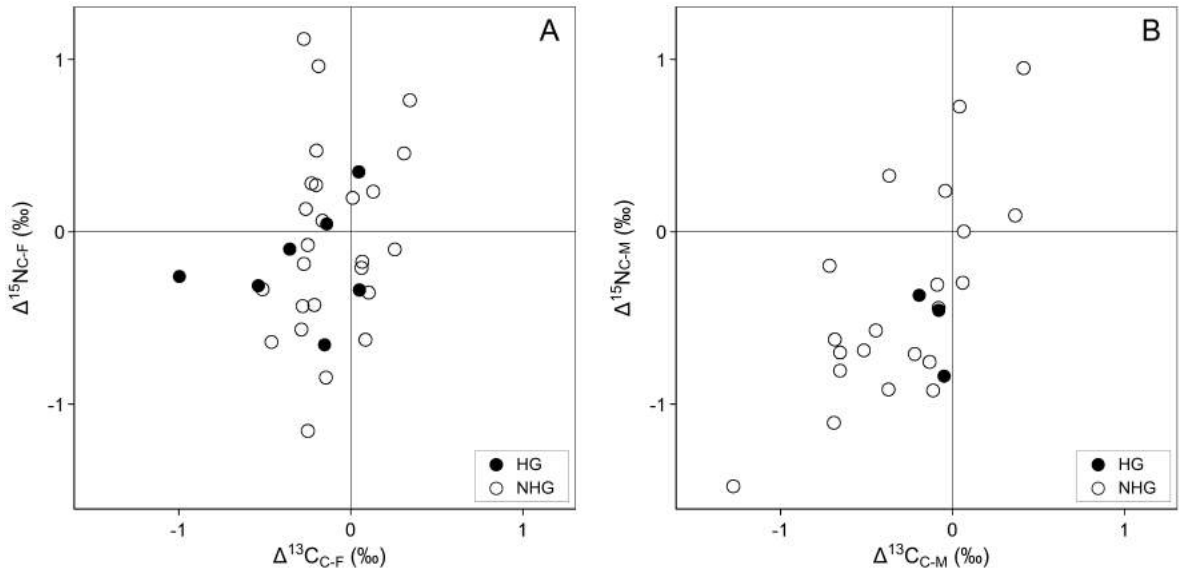

Figure 3. Scatterplot of (A) $\delta^{13}C$ and (B) $\delta^{15}N$ differences between PWC and adult females/males for the archaeological populations.

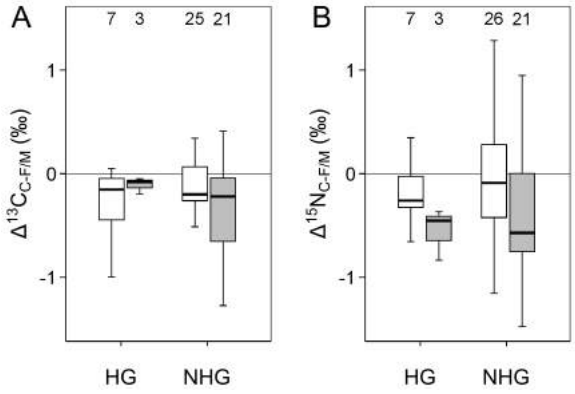

Figure 4. Boxplot of (A) $\delta^{13}C$ and (B) $\delta^{15}N$ differences between adult females/males and PWC for the archaeological populations. Empty and shaded boxes indicate isotopic differences between adult females and males, respectively. Numbers above the boxes indicate the sample size.

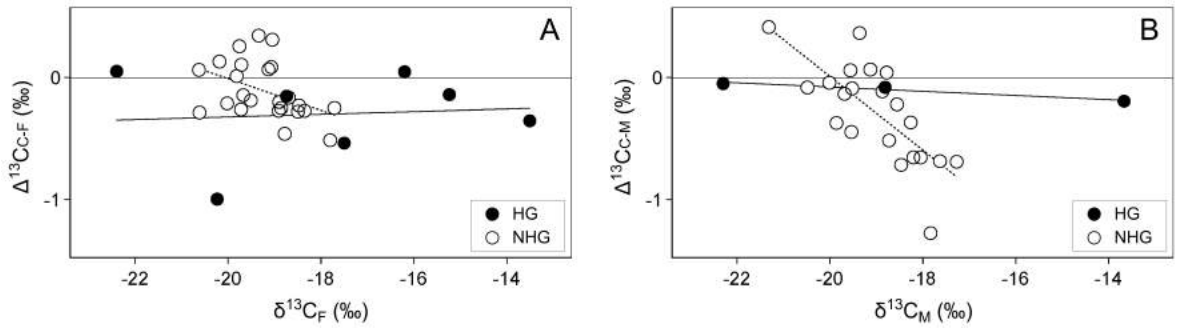

Figure 5. Relationships between adult $\delta^{13}C$ values and $\delta^{13}C$ differences between PWC and adults for (A) females and (B) males. Solid ($\Delta^{13}C_{C\text{-}F} = 0.01 \times \delta^{13}C_F - 0.11$ and $\Delta^{13}C_{C\text{-}M} = -0.02 \times \delta^{13}C_M - 0.42$) and dotted ($\Delta^{13}C_{C\text{-}F} = -0.13 \times \delta^{13}C_F - 2.61$ and $\Delta^{13}C_{C\text{-}M} = -0.30 \times \delta^{13}C_M - 6.02$) regression lines indicate relationships in HG and NHG populations, respectively.

TABLES

Table 1. Mean, SD, population number, and statistics of paired Mann−Whitney U test of $\delta^{13}C$ and $\delta^{15}N$ differences between adult females and males.

Subsistence	Variable	Mean	SD	n	U	P value
HG	$\Delta^{13}C_{M-F}$	-0.10	0.60	6	10	1.000
	$\Delta^{15}N_{M-F}$	0.33	0.61	6	5	0.313
NHG	$\Delta^{13}C_{M-F}$	0.16	0.34	27	72	0.004
	$\Delta^{15}N_{M-F}$	0.25	0.54	28	75	0.003

Table 2. Mean, SD, population number, and statistics of paired Mann−Whitney U test of $\delta^{13}C$ and $\delta^{15}N$ differences between PWC and adult females/males.

Subsistence	Variable	Mean	SD	n	U	P value
HG	$\Delta^{13}C_{C-F}$	-0.30	0.37	7	25	0.078
	$\Delta^{13}C_{C-M}$	-0.11	0.08	3	6	0.250
	$\Delta^{15}N_{C-F}$	-0.18	0.32	7	21	0.297
	$\Delta^{15}N_{C-M}$	-0.55	0.25	3	6	0.250
NHG	$\Delta^{13}C_{C-F}$	-0.11	0.23	25	243	0.030
	$\Delta^{13}C_{C-M}$	-0.29	0.41	21	200	0.002
	$\Delta^{15}N_{C-F}$	0.02	0.60	27	187	0.972
	$\Delta^{15}N_{C-M}$	-0.39	0.61	21	184	0.016

Table 3. Mean, SD, population number, and statistics for paired Mann−Whitney U test of $\delta^{13}C$ and $\delta^{15}N$ differences between PWC−adult male differences and PWC−adult female differences.

Subsistence	Variable	Mean	SD	n	U	P value
HG	$\Delta^{13}C_{C\text{-}M}-\Delta^{13}C_{C\text{-}F}$	-0.04	0.13	3	2	0.750
	$\Delta^{15}N_{C\text{-}M}-\Delta^{15}N_{C\text{-}F}$	0.19	0.36	3	5	0.500
NHG	$\Delta^{13}C_{C\text{-}M}-\Delta^{13}C_{C\text{-}F}$	0.18	0.31	21	201	0.002
	$\Delta^{15}N_{C\text{-}M}-\Delta^{15}N_{C\text{-}F}$	0.24	0.59	21	179	0.026

Table 4. Best-fit models for PWC−adult differences.

Subsistence	Response	Explanatory	Estimate	SE	t	P	AIC
HG	$\Delta^{13}C_{C\text{-}F}$	(Intercept)	-1.04	0.40	-2.58	0.062	7.38
		$\Delta^{15}N_{C\text{-}F}$	0.58	0.42	1.40	0.234	
		t_2'	0.19	0.09	2.09	0.105	
	$\Delta^{15}N_{C\text{-}F}$	(Intercept)	0.68	0.55	1.25	0.279	7.14
		$\Delta^{13}C_{C\text{-}F}$	0.56	0.40	1.40	0.234	
		t_2'	-0.15	0.10	-1.53	0.202	
NHG	$\Delta^{13}C_{C\text{-}F}$	(Intercept)	-3.63	1.11	-3.27	0.003	-5.98
		$\delta^{13}C_F$	-0.16	0.05	-2.96	0.007	
		$\delta^{15}N_F$	0.04	0.02	2.13	0.044	
	$\Delta^{13}C_{C\text{-}M}$	(Intercept)	-4.12	1.19	-3.47	0.003	3.56
		$\delta^{13}C_M$	-0.21	0.06	-3.39	0.003	

	$\Delta^{15}N_{C-M}$	0.31	0.10	3.05	0.007	
$\Delta^{15}N_{C-F}$	(Intercept)	-0.05	0.11	-0.42	0.677	44.62
$\Delta^{15}N_{C-M}$	(Intercept)	-0.08	0.12	-0.68	0.506	28.63
	$\Delta^{13}C_{C-M}$	1.06	0.24	4.42	0.000	